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PHYTOPATHOLOGY

VOLUME X NUMBER 12

DECEMBER, 1920

STUDIES ON THE RATE OF GROWTH AND BEHAVIOR OF THE BLISTER RUST ON WHITE PINE IN 1918

ARTHUR S. RHOADS

The field studies upon which this paper is based were conducted by the writer at Kittery Point, Maine, during the spring and summer of 1918, as part of the campaign of intensive field investigations on the white pine blister rust directed by Dr. Perley Spaulding of the U. S. Bureau of Plant Industry. These studies were undertaken with a view to determining the rate of growth and behavior of the blister rust cankers, and to gain a better conception of the ecology of this very important parasite. Although based on the work of but a single year in a single locality, the results in general are believed to be typical of the rate of growth and behavior of the blister rust on white pine.

EXPERIMENTAL METHODS

During the last week in April, the beginning of aeciospore dissemination, and the first week in May, one hundred and thirty-three cankers, ranging from the smallest to the largest on the trunks, branches, and twigs of one hundred trees, were outlined by a narrow band (about $\frac{1}{8}$ inch in width) of white lead paint.[1] Each canker was marked by a number painted near it, and the location of each of the one hundred trees bearing the cankers outlined for study was plotted to scale on a map.

The trees in question ranged in age from nine to twenty-five years, in diameter from $\frac{5}{8}$ inch to 9 inches at 1 foot elevation, and in height from $2\frac{1}{2}$ to 30 feet; they were mostly trees in the open that showed little or no tendency to suppression. In addition to the tree description, a full description was made of the individual cankers at the beginning of the

[1] No injurious effect of the white lead paint on the bark was noted, and its superficial application is not believed to have had any effect on the growth of the young mycelium at the outer edges of the cankers, since this occurs mostly in the inner portion of the bark. In many cases aecia burst through the bark directly beneath the narrow band of paint.

study. Along with the latter data a study was made of such points as the origin of the infection; its position on the stem, that is, whether it had occurred at the node or internode, and its location by whorls of branches counted down from the top; the center and extent of the actively fruiting cankers by whorls of branches; the size of the diseased stem in contrast to the size of the normal stem estimated at the same point; the extent of both the past and present aecial areas, together with the abundance of aecia on the 1918 fruiting area; and other points bearing on the increase in size, during the growing season of 1918, of the various zones usually exhibited by the cankers during the different stages of their development. In addition to the points enumerated above, full notes were made from time to time on the death of the trees or branches of the trees, resulting from the normal growth of the fungus, or from attacks by insects or secondary fungi.

The cankers were outlined at the outer limits of the etiolated zone of bark, which roughly marks the tips of the invading mycelium. In the early spring there was a pronounced etiolated zone, usually extending well beyond the pycnial zone of the preceding year, on which latter area the 1918 growth of aecia was starting to develop.

The second series of measurements was made during the last week in July, nearly two months after the beginning of the 1918 pycnial development. At this season of the year there was but very little or no etiolated bark to be seen beyond the pycnial zone, since the new pycnial area had developed over the areas previously etiolated on the cankers. A dotted line was painted about the edge of the etiolated zone, or about the outer edge of the pycnial zone in case the etiolated zone did not extend beyond the pycnial zone. Measurements were made up and down, and to the left and right, from the original painted line in case the canker had not by this time completely encircled the stem on which it was developing. In making the measurements the writer was careful to take them between the centers of the two lines; in this way cumulative errors in the measurements, due to the unavoidable thickness of the line of paint, were avoided. The trees bearing the numbered cankers were under almost daily observation from the latter part of April to the end of July.

During the second week in September the writer returned to Kittery Point in order to again outline the cankers and to complete a third series of measurements on their growth. At this time the majority of the cankers were still producing pycnia abundantly.

At the beginning of the study the problem of securing reliable data for an index of the rate of growth of the blister rust was thought to be a long-term proposition, but the advance of the cankers during the growing season of the host was so decided that the results of the first season's study are deemed worthy of publication.

BEHAVIOR OF PYCNIA AND AECIA

Pycnia develop on the etiolated zone of bark at the edge of the canker, just beyond the aecial zone, which, if present, is developed earlier in the same year. The production of pycnia began the first week in June and continued steadily until September 10, the date when the last observation was made. It has been the experience of others that the production of pycnia continues until the beginning of winter.

Aecia are produced in the spring with the advent of warm weather and, as a rule, are produced in varying degrees of abundance. They occur chiefly on the pycnial area of the preceding year. On some cankers no aecia may be produced, and on others their development may be so great that they not only fruit all over the pycnial area of the preceding year but extend considerably beyond it. In one case observed, within a little over two weeks after the outer limits of a canker had been outlined on the trunk of a tree $2\frac{3}{4}$ inches in diameter, the aecial area jumped beyond the line and burst out from under the bark which, previously, had neither produced pycnia nor shown any etiolation, and extended for a distance of 3 inches below the lower limit of the canker as originally outlined, thus bringing it down to the ground line.

Early in the season of aecial fruiting the writer started an experiment to determine just how long the individual aecia disseminate spores. On May 3, three hundred pins, each bearing its number on a piece of paper, were carefully stuck into as many different aecia on a total of twenty-two trees representing an even larger number of cankers. The pins were placed only in those aecia that had either just started or were practically ready to break open. By May 20 the peridia of all but sixty-three of the aecia were well ruptured or lost entirely, together with most of the spore mass. On May 29 only nineteen aecia still retained their peridia, and on June 4 only four of these had preserved their peridia. In the latter case the retention of the peridia was abnormal, the entire aecium being either sealed over with a crust of resin or held in place by tightly appressed bark scales. From the behavior of the three hundred aecia under study it is evident that they attain the climax of their development within less than two weeks after the peridia start to break open, and then begin to decline rapidly. Spore production seems to be mostly over with the maturity of the aecium and the rupture of its peridium. After this stage of development is reached the aeciospores gradually become disseminated. Aeciospore dissemination may be regarded as practically at an end within four weeks after its start, the heaviest part of it being over in two weeks.

After the climax of the aecial development has passed, a few sporadic aecia may later develop out beyond the main fruiting zone. Such pustules, as a rule, are of smaller size than the majority of those first formed.

Quite frequently aecia were observed on old aecial areas that had fruited the preceding year, and, in some few cases, even earlier. Such fruiting seems to be confined to isolated areas where the vitality of the bark was not entirely depleted by the previous production of aecia.

On trees where the infection has been of long standing and its point of origin not too high, the aecia develop down the trunk to the ground line, and often continue their development down onto the roots and even fruit several inches below the surface of the duff and soil.

RATE OF GROWTH OF THE BLISTER RUST ON WHITE PINE

During the period of four and one-half months for which the growth of the blister rust cankers was computed, a number of potential measurements were lost unavoidably. In some cases entire measurements were lost due to the death of certain trees and parts of trees bearing the measured cankers, as a result of the disease itself, insect attacks, and the breaking of branches. An even larger number of measurements of the downward growth of the cankers was invalidated, since many of the cankers near the base of the trunks grew down to the ground line before the end of the season, so that in such cases the complete record of growth in this direction could not be obtained satisfactorily. Of the measurements on the spread of the cankers around the stems, but few were obtained, since most of the cankers had already encircled the stems at the beginning of the aecial season and the majority of the remainder did so soon after the initial measurements were made. The complete growth records available for the whole season from May 1 to September 10 may be briefly summed up as follows:

One hundred and thirteen measurements on upward growth gave an average figure of 2.44 inches; seventy-seven measurements on downward growth gave an average figure of 2.57 inches. The total vertical growth of the cankers, both up and down, therefore averages 5 inches. Twelve measurements of the circumferential growth of the cankers to the left gave an average figure of 1.17 inches; thirteen measurements of the same type of growth to the right gave an average of 1.33 inches. The lateral or circumferential growth of the cankers, both to the left and right, therefore averages 2.5 inches, or one-half that of the vertical growth. Unfortunately, but few measurements of growth in the lateral direction were to be had, due to the rapidity with which the disease encircled the small stems at the infected point.

In general it may be said that the growth of the blister rust cankers is in direct proportion to the size and vigor of the stems on which they occur. Cankers on the lower and usually smaller branches, either shaded or unshaded, develop very slowly. Shading apparently has little effect on their development.

The rate of growth of individual cankers is quite a different matter from the average rate of growth of a large number. A few cankers that made no growth during the period from May 1 to July 31 advanced considerably after that date. On the other hand, a few that made considerable growth during this period made none during that between August 1 and September 10. Still a few other cankers made no advance during the entire summer, although they produced aecia sparingly in the spring. The greatest upward growth noted between May 1 and September 10 on any one canker was 6 inches; the greatest downward growth noted during this period on any one canker was 8 inches.

A comparison of the growth figures for the first three-month period, from May 1 to July 31, shows that the average vertical growth was approximately the same in both directions and constituted approximately 50 per cent of the total vertical growth of the whole period from May 1 to September 10. The average lateral growth of the first three-month period was approximately the same in both directions, but constituted 70 per cent of the total lateral growth of this whole period. Comparison of the lateral growth of these periods, however, is less certain than that of the vertical growth, as the former is based on vastly fewer figures than the later. In general it may be said that the growth of the blister rust cankers for the one and one-half month period in the latter part of the summer was as great as that of the three-month period in the spring and early part of the summer; in other words, during the latter part of the summer growth was twice as fast as that during the spring and early part of the summer. It is likely that the rate of growth of the blister rust on white pine is influenced chiefly by temperature. That temperature is in all probability the chief climatic influence in determining the rate of growth of the chestnut blight fungus (*Endothia parasitica*), a bark-inhabiting parasite, has been shown by Stevens (5).

The above figures for the growth of the blister rust cankers (5 inches for total vertical growth and 2.5 inches for total lateral growth) from May 1, 1918, to September 10, 1918, do not constitute a reliable index of the total annual growth, since more or less vegetative growth of the blister rust fungus may be expected to occur between early September and the end of April, particularly between early September and the beginning of winter. The advent of winter does not completely inhibit the vegetative growth of many of the wood- and bark-inhabiting fungi,

since many of them will grow at temperatures of but a few degrees above the freezing point. For example, Stevens (4) states that field observations and laboratory experiments both show that the chestnut blight fungus (*Endothia parasitica*) will grow whenever the temperature rises above the minimum for growth, which, as Shear and Stevens (3) have determined, is about 8° or 9°C. As Stevens (4) states, this apparently is true regardless of the previous temperature and whether the host is dormant or not.

Mr. G. F. Gravatt, while at Kittery Point early in September, 1919, outlined with paint and remeasured a number of the cankers marked by the writer in May, 1918. In a recent communication he reports that the average growth from May 1, 1918 to September 10, 1918, of the thirty-five cankers which he remeasured was 2.7 inches, whereas the average growth from September 10, 1918 to September 6, 1919, was 4.11 inches, based on the same thirty-five cankers measured at the same points. Most all of these measurements were of growth up the stem. Unless a study of the weather conditions, particularly the temperature, shows a great difference between 1918 and 1919, it must be assumed that the blister rust makes considerable growth between September 10 and May 1. It is to be expected, however, that the majority of this growth will take place between September 10 and the beginning of winter. Judging from the remeasurement figures furnished by Mr. Gravatt, the growth figures from May 1 to September 10 given the writer as an average for cankers of various sizes, represent about two-thirds of the total annual growth of the blister rust cankers.

In table 1 the available figures on the vertical growth of the blister rust cankers from May 1 to September 10 have been correlated with the size of the stems on which they occurred. From this condensed presentation of the figures it is evident that the larger the stems, within the limits given, the greater is the growth of the cankers, in a vertical direction at least.

As only a single tree fell in the "4.1–5.0" diameter class, this individual was omitted from the comparison. This table likewise analyzes the rate of downward growth in comparison to that of the upward growth of the cankers. It shows a tendency, in all but the last diameter class, for the downward growth to exceed the upward growth in cankers falling in the same diameter class.

Many of the largest cankers on the trunks and older branches are formed as a result of two or more branch infections which run back into the main stem either simultaneously or at different times. The result is that a canker of unusual length is ultimately formed. The longest canker noted on a branch was on a twenty-five-year-old tree. In the

spring of 1918 this canker was already 42 inches long and had part of the old aecial area eaten off by squirrels; during the summer of 1918 it extended its length nearly 4 inches. The two lateral branches, through which infection entered simultaneously, died during the summer, but the main branch with a canker 46 inches in length was still living at the end of the season. It was only $1\frac{3}{8}$ inches in diameter but had enlarged to 2 inches at the center of the canker; the age of the infected portion varied from eight to twelve years.

TABLE 1

Correlation of the vertical growth of the cankers, from May 1 to September 10, with the size of the stems on which they occurred

DIAMETER CLASSES OF STEMS	AVERAGE TOTAL GROWTH UP	NUMBER OF CANKERS BASED ON	AVERAGE TOTAL GROWTH DOWN	NUMBER OF CANKERS BASED ON	TOTAL AVERAGE VERTICAL GROWTH
inches	*inches*		*inches*		*inches*
0.1–0.5	0.75	16	1.35	16	2.10
0.6–1.0	1.57	24	2.06	22	3.63
1.1–2.0	2.90	31	3.09	22	5.99
2.1–3.0	3.03	30	3.42	12	6.45
3.1–4.0	3.55	14	3.42	6	6.97

The longest canker noted on the trunk was one on a 2-inch tree that had enlarged to $2\frac{1}{4}$ inches at the center of the infection. In the spring of 1918 the canker had attained a length of 39 inches, apparently all this growth resulting from a single infection, and had grown down to the base of the tree, thereby rendering further growth in this direction difficult to measure. The age of the infected portion of the stem ranged from ten to thirteen years. This tree, which had withstood the attack of the blister rust for so long, finally succumbed early in the summer of 1918.

PATHOLOGICAL EFFECT OF THE BLISTER RUST ON WHITE PINE

White pine blister rust cankers may result in either a swelling or a constriction of the pine stem; both symptoms may be of equal prominence on the different stems. That there is a regular occurrence of, and a definite relation between, the swelling and constriction of the pine stems does not seem to have been pointed out clearly, the two having been regarded largely as pathological symptoms of more or less haphazard occurrence.

The writer's field studies indicate that infected twigs and the smaller stems up to 2 inches in diameter, as a rule, exhibit swelling which is proportionately greater the smaller the stem, and that infected stems of about 2 inches or more in diameter rarely become swollen but either remain normal in outline or become constricted, depending upon the age

of the infection. As a rule infected stems of this size retain their normal diameter for a time and become constricted only after the cankers have developed for a long time. With the continued development of the blister rust cankers on these larger stems the constriction becomes more and more pronounced until the girdling is sufficient to completely retard conduction in the stem and its death ensues. The reason for the difference in pathological symptoms, namely, swelling in comparatively young cankers on the smaller stems, and constriction in the case of the older cankers on larger stems, are readily understood when one makes a stem analysis of the lesions.

According to Colley (2), the mycelium of the white pine blister rust is confined almost entirely to the region of the cortex and phloem cells, although the hyphae do enter the rays and occasionally work their way in between the tracheids so that they have been traced to a depth of three annual rings, counting in from the cambium.

In the early stages of the disease the etiolation of the bark and its subsequent swelling are the first prominent pathological symptoms of stem infection. The swelling is confined to the bark alone, and, according to Colley (2), is due to the fact that the abundant mycelium of the parasite forces apart the phloem and cortex cells of the host, rather than to any increased subdivision of the bark cells.

On larger stems of about 2 inches in diameter, where the cankers develop for a longer period by reason of the fact that the stems are not killed so quickly, the formation of the annual ring becomes retarded and the annual accretion of wood at the central transverse plane of the canker diminishes gradually, often in peripheral extent rather than in thickness. On stems of about 2 inches in diameter the loss of normal accretion is often just about sufficient to compensate for the abnormal thickness of the diseased bark, so that the stem still retains a symmetrical outline; consequently no external indication of the abnormality, other than the diseased appearance of the bark, appears in the stem of the tree at the point where the lesion occurs.

On cankers of long standing, which usually occur on stems of two inches or more in diameter, there is a marked falling off in the normal accretion of the wood occurring simultaneously with the progress of the disease. It often happens that the annual ring fails to develop entirely around the stem at the central point of the lesion in a given year, and each successive ring is less extensive until finally, with the death of the tree or even before, none is formed. Such growth results in trees of very irregular outline in cross section at the center of the lesion.

STEM ANALYSIS OF WHITE PINES KILLED BY THE BLISTER RUST

Early in July a stem analysis was made on twenty-eight white pines killed by the blister rust. The trees dissected were located on the main infection area used for the study of the rate of growth of the cankers. Of these trees a few, also used for the growth study, had died just prior to the dissection study; most of them, however, had been dead for about a year. The tree description and infection data were made as in the growth study, and these data, together with the stem analysis measurements, are presented in table 2.

The stem analysis measurements were obtained by sawing off the trunk through the center of the canker responsible for the death of each tree. The theoretical age of the stem at this point was obtained by a count of the whorls of branches down from the top. In every case this age count was found to agree with the check derived by a ring count of the normal wood, either above or below the canker, plus the number of nodes (usually only one or two) that it was necessary to go above the canker, or minus the number it was necessary to go below the canker to make a cut suitable for determining the age of the normal wood.

The figures in the column headed "Age of wood actually formed at center of canker" were obtained by counting the total number of growth rings on the transverse section made through the center of the canker. As will be noted, they vary greatly according to the direction of the count, since, as previously stated, in old cankers the annual accretion of wood often fails to develop uniformly around the whole stem, and each succeeding ring becomes less and less extensive until finally, either with or before the death of the tree, none is formed.

The figures in the column headed "Probable age of stem at center of canker at time of infection" could be determined in the field only by the appearance of the annual rings of growth as revealed by the smoothed transverse section of the canker through its central point. The irregularity of the growth rings and their impregnation with resin was found to be a fairly reliable index of the presence of the blister rust after it had attained sufficient development to produce aecia more or less abundantly. There is no reason to believe that the incipient stages of the blister rust have any marked effect on the annual accretion of wood, at least none that would be visible macroscopically. The exact date of stem infection, of course, could be told only by means of a microscopic examination of sections of the wood for the presence of the mycelium. Even such refined procedure would perhaps not accurately establish the exact date of infection, for, though it is likely that the mycelium is to be found in the ray cells of the annual ring laid down the same season that infection took

place, it might spread in along the medullary ray cells for a ring or two toward the center of the stem before the death and consequent infiltration of the wood elements might occur at the point of infection. It is evident that the figures given for the probable age of the different stems at the time infection took place are but a rough index of the time when

TABLE 2

Summary of a stem analysis of white pines killed by the blister rust

TREE DESCRIPTION			DIAMETER OF STEM IN INCHES AT CENTER OF CANKER		SPREAD OF CANKER UP	SPREAD OF CANKER DOWN	AGE OF INFECTED PORTION OF STEM, COUNTED BACK FROM THE TOP	THEORETICAL AGE OF STEM AT CENTER OF CANKER	AGE OF WOOD ACTUALLY FORMED AT CENTER OF CANKER	PROBABLE AGE OF STEM AT CENTER OF CANKER AT TIME OF INFECTION	DIFFERENCE BETWEEN THEORETICAL AND GREATEST ACTUAL AGES OF STEM AT CENTER OF CANKER	YEARS REQUIRED TO KILL TREE AFTER CANKER SPREAD TO MAIN STEM.	AVERAGE DIAMETER OF INFECTED WOOD AT CENTER OF CANKER
Height	Diameter at height of 1 foot	Age	Estimated normal diameter	Actual diameter									
feet	*inches*	*years*	*inches*	*inches*	*inches*	*inches*	*years*	*years*	*years*	*years*	*years*	*years*	*inches*
10.0	3.2	16	3.5	3.2	16.0	12 0*	10–16	12	12	7–8	0	4–5	2.7
10.0	2.0	14	2.7	2.0	10.0	12.0	10–13	11	9 x 10	7–8	1	3–4	1.9
10.0	2.0	14	2.5	1.9	12.0	17.5	10–13	11	8	5–6	3	5–6	1.6
7.5	3.0	13	2.5	3.0	12.0	11.0*	9–13	11	10	9	1	2	2.2
14.0	3.0	14	3.0	2.6	12.0	14 0	10–14	11	8 x 10	7–8	1	3–4	2.2
12.0	2.1	15	2.5	2.1	10.0	10.0	9–10	9	6 x 7	5–6	2	3–4	1.9
15.0	3.4	15	3.5	2.7	7.5	8 5	11–13	11	7 x 11	7	0	4	2.5
15.0	2.2	9	2.2	2.2	19.0	10 0*	12–15	12	9 x 11	8	1	4	1.9
5.0	0.6	11	0.6	0.8	4.0	5.0	8–9	8	8	7	0	1	0.7
9.5	1.4	12	1.4	1.4	17.0	10.0	8–10	9	9	8	0	1	1.3
7.0	2.5	15	2.5	2.4	10.0	8.0*	10–15	11	9 x 11	8–9	0	2–3	2.0
8.0	2.5	14	2.6	2.5	10.0	6.0*	11–14	12	10 x 11	8	1	4	2.1
8.5	3.5	14	3.5	3.5	22.0	8.0*	10–14	12	9 x 11	7–8	1	4–5	2.7
5.0	1.1	13	1.4	1.5	10.0	5.0*	9–13	11	10 x 11	8–9	0	2–3	1.2
5.0	1.2	9	1.2	1.5	15.0	6.0*	6–9	7	7	5	0	2	1.1
12.0	3.7	14	3.7	3.4	10.0	3.0*	10–14	12	7 x 11	6–7	1	5–6	2.9
18.0	4.5	16	4.5	4.2	9.0	14.0*	12–16	13	9 x 12	8–9	1	4–5	3.6
6.0	1.4	15	1.2	1.4	7.0	4.0*	12–15	14	9 x 13	8	1	6	1.1
8.5	1.7	14	1.5	1.6	12 0	12 0	8–11	9	7 x 8	5	1	4	1.2
8.0	2.2	14	2.2	1.6	17.0	4.0*	10–14	13	8 x 9	7	4	6	1.4
10.0	2.5	15	2.7	2.7	12.0	7.0*	10–15	12	9 x 12	8–9	0	3–4	2.2
10.0	3.0	14	3.2	3.0	22.0	6.0*	10–14	12	8	7	4	5	2.2
6.0	2.2	13	2.5	2.2	20.0	8.0*	9–13	10	9	7	1	3	2.0
7.5	2.5	14	2.5	2.2	17.0	5.0*	10–14	12	7 x 11	6–7	1	5–6	1.7
7.0	1.7	13	2.0	1.5	10.0	10.0	8–12	9	7 x 9	6–7	0	2–3	1.1
12.0	2.5	15	2.7	2.5	27.0	6.0*	11–15	13	8 x 10	8	3	5	2.0
13.0	2.5	13	2.5	2.2	17.0	10.0*	11–13	12	10 x 12	8–9	0	3–4	1.9
13.0	3.7	14	3.7	3.0	10.0	15.0*	12–14	12	7 x 10	6–7	2	5–6	2.6

* Down to ground line.

the infection developed sufficiently on the stem to cause the annual accretion of wood to become abnormal.

By subtracting the greatest number of rings actually formed at the center of the canker from the theoretical age of the stem at this point, which, as explained in the third preceding paragraph, was derived from a count of the whorls of branches and checked by a ring count made on the normal wood, either above or below the canker, and corrected for the loss or gain of age incurred by making the count either one year's growth above or below respectively, there will be found in a number of cases a difference of as many as one, two, three, and even four years. No evidence of any false ring formation was detected in any of the transverse sections and, furthermore, the age of each stem at the point of its infection was checked by a count, made from the top down, of the whorls of branches. This difference between the theoretical and actual ages of the stem at the center of the canker can therefore be explained only on the ground that the growth of the wood around the stem had ceased in the vicinity of the center of infection, but that the increment continued on the stem both above and below the canker. It is likely that, after a certain length of time, the cambium about the canker was too badly weakened to make any further contribution to the xylem portion of the stem, or, if any further growth took place, it was so slight that its detection was impossible macroscopically. Normal additions to the stem, however, continued to be put on both above and below the canker. From this it is evident that there was no complete girdling of the stem at the center of the canker. The power of cell division of the cambium about the canker had practically or entirely ceased, unless we consider the possibility of the formation of a secondary phloem.

The above measurements indicate that the retention by the stem of its conductive power varies from one to as many as four years after the cessation of any material wood formation at the center of the canker before the death of the tree ensued. It is this cessation in the growth of the xylem at the center of the canker, and its continuance both above and below the lesion, that cause the marked constricted appearance commonly exhibited by infections of long standing on the older stems despite the partial compensation afforded by the presence of the greatly thickened bark covering the lesions.

Continuing with table 2, the column marked "Years required to kill tree after canker spread to main stem" is obtained by subtracting the figures in the column headed "Probable age of stem at center of canker at time of infection" from that headed "Theoretical age of stem at center of canker." For the reasons mentioned in the third preceding paragraph, this result probably is too low by at least two years. The results given.

however, are approximate and indicate that the white pine blister rust, on the larger stems at least, is a comparatively slow-working disease, although nevertheless a very potent factor in killing young white pines.

The column headed "Average diameter of infected wood at center of canker" gives the diameter of the stem inside the bark on the transverse section made at the center of the canker, and, when subtracted from the column giving "Actual diameter" and the result divided by two, some idea may be had of the thickness of the bark on old blister rust cankers for stems of different sizes.

BIOLOGIC RELATION OF COMPETITIVE SECONDARY FUNGI TO THE WHITE PINE BLISTER RUST

As was noted by Messrs. G. B. Posey and G. F. Gravatt during their work at Kittery Point in the summer of 1917, a number of miscellaneous secondary fungi frequently play an important rôle in interfering with the normal development of the blister rust on white pine. Not infrequently such secondary fungi may be so rapid in their growth that they overrun the blister rust lesion and completely suppress the rust so that it fails to develop pycnia and aecia. As a general rule the blister rust lesion invaded by the secondary fungus becomes constricted, and often very sharply so, even on small stems. In general it may be said that lesions caused by these so-called "secondary fungi," either alone or in combination with the blister rust, present quite a different appearance than lesions caused by the blister rust alone. From numerous observations made on the occurrence of these secondary fungi associated with the blister rust, it is evident that certain of them are quicker and more potent agencies in girdling the branch or stem than the blister rust alone. The majority of them, however, are very weak parasites and only retard the fruiting and rapidity of the mycelial growth.

SCOLYTID ATTACKS RESPONSIBLE FOR HASTENING THE DEATH OF WHITE PINES INFECTED BY BLISTER RUST

As a contributing cause of the accelerated death of white pine trees infected by blister rust, the rôle of a scolytid beetle, *Pityogenes hopkinsi* Swaine,[2] is of considerable importance, at least in the vicinity of Kittery Point. On May 10 the writer first noted the presence of the adults on the trunks and branches of young white pines, and in a few days they were present in comparatively large numbers, beginning the work of excavating

[2] Determination by Dr. A. D. Hopkins of the U. S. Bureau of Entomology, Washington, D. C.

their tunnels, which resulted in the formation of numerous little heaps of "sawdust" all over many of the trunks. About three weeks after this the insect-infested trees suddenly commenced to die rapidly. Few other white pines on this area died at this time. Even those practically girdled by the blister rust, but not attacked by the scolytids, did not die as a rule until mid-summer, when the transpiration pull on them was greater, and then death was a comparatively slow and gradual process compared to that of the white pines attacked by insects. A careful study of the effect of *Pityogenes hopkinsi* in relation to the blister rust epidemic on the area under study showed that the attacks of this scolytid were limited entirely to such white pines as had their vitality more or less lowered by the presence of one or more blister rust lesions on the vital part, namely the trunk. In some cases the lesions had been invaded previously by a secondary fungus which had completely retarded the production of aecia. Such a relation between the general lack of vigor of the host tree and its attack by this species has been indicated by Blackman (1), although the white pine blister rust was not mentioned as one of the causes contributing to the insect attack. The attacked trees were all young ones, ranging in diameter from 1 to 4 inches and still retaining the thin smooth bark characteristic of young white pines. Many of the trees attacked by the beetles had not then been seriously affected by the blister rust. At the time of their attack by the insects, several still presented a thrifty appearance, and, without the interference of the insects, would not have died for at least from one to three years. *Pityogenes hopkinsi*, therefore, may be responsible at times for expediting the death of white pines infected by the blister rust.

SUMMARY

From the behavior of three hundred aecia under study on various cankers it is evident that they attain the climax of their development within less than two weeks after the peridia start to open, and then begin to decline rapidly. Aeciospore dissemination may be regarded as practically at an end within four weeks after its start, the heaviest part being over within two weeks under normal conditions.

During the period from May 1 to September 10 the vertical growth of the blister rust cankers, both up and down, averaged 5 inches. During the same period the lateral growth, both to the left and right, averaged 2.5 inches, or one-half that of the vertical growth. It is likely that these figures represent about two-thirds of the total annual growth of the blister rust cankers.

Growth of the cankers during the latter part of the summer was twice as fast as that during the spring and early part of the summer. It is

likely that the rate of growth of the blister rust on white pines is influenced chiefly by temperature.

The vertical growth of the blister rust cankers, when correlated with the size of the stems on which they occurred, indicates that the larger stems, up to 4 inches in diameter, the greater is the growth of the cankers. There is also shown for stems of 3 inches or less in diameter a general tendency for the downward growth to exceed the upward growth in cankers falling into the same diameter class.

A stem analysis of white pines killed by the blister rust reveals that infected twigs and smaller stems, up to about 2 inches in diameter, exhibit swelling which is proportionately greater on the smaller stems and solely due to the abnormal thickening of the bark. In the case of cankers of long standing on the older stems, usually those of 2 inches or more in diameter, however, the stem rarely becomes swollen but usually remains normal in outline or, in cankers of especially long standing, becomes constricted. The latter often exhibit a marked diminution in the increment of the stem at the center of the canker, which is often compensated for, in so far as the outline of the stem is concerned, by the abnormally thickened bark.

In the older cankers the number of growth rings formed at the center of the canker may be one, two, three, or even four, years less than the theoretical age of the stem at this point, based on the age of the wood both above and below the canker. This indicates that the retention by the stem of its conductive power may vary from none to as many as four years after the cessation of any material wood formation at the center of the canker before the death of the tree ensues.

A number of miscellaneous secondary fungi play an important rôle in interfering with the development of the blister rust. Such fungi, which are mostly of the nature of weak parasites, may be so rapid in their growth as to overrun the blister rust lesion and retard, more or less completely, the production of pycnia and aecia, as well as the growth of the mycelium.

Attacks by a scolytid beetle, *Pityogenes hopkinsi*, were responsible for expediting the death of a number of white pines infected by blister rust. The attacks of this beetle were limited entirely to such white pines as had their vitality more or less lowered by the presence of one or more blister rust lesions on the trunk.

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A FOURTH PHYTOPHTHORA DISEASE OF TOMATO

DONALD REDDICK

Three diseases of tomato (*Lycopersicon esculentum*) caused by species of *Phytophthora* have been described. These are blight,[1] caused by *P. infestans*, buckeye rot of fruit[2] caused by *P. terrestria*, and foot rot or collar rot,[3] caused by *P. cryptogea*. A fourth disease caused by a species of *Phytophthora* occurs on tomatoes grown under glass in the vegetable houses at Cornell University. Plants of both winter and spring crops have been somewhat affected each year for a number of years. The disease has been noted by several persons but has not been an object of more than passing study until now.

Name. This disease has so many manifestations that a single name is not comprehensive enough to include all phases. The most characteristic symptom is a girdling of the stem and for convenience the name stem-girdle will be used in referring to it.

Symptoms. Briefly, the following symptoms may be noted: (a) typical damping off of seedlings; (b) a girdling of stems of all ages and at any point, with subsequent collapse of the plant above the lesion; (c) blight of foliage, usually in limited areas but occasionally involving one or more leaflets; (d) a rapid rot of fruit; (e) gradual death of foliage from the base and eventual death of the plant as a result of late root infection.

Distribution and losses. There seems to be no other record of the occurrence of this disease either in greenhouses or in fields. I. C. Jagger states, in correspondence, that the disease was not encountered by him in his rather extended investigations of truck crop diseases in New York, including observations made in the greenhouses at Irondequoit, New York, a region of intensive production under glass. In the houses at Ithaca the losses have been estimated at times as involving half the crop—enough to

[1] Reed, Howard, S. Tomato blight and rot in Virginia. Virginia Agric. Exp. Sta. Bull. 192, 16 p. 1911. See also, Giddings, N. J., and Anthony Berg. A comparison of the late blights of tomato and potato. Phytopath. **9:** 209–210, pl. 11. 1919.

[2] Sherbakoff, C. D. Buckeye rot of tomato fruit. Phytopath. **7:** 119–129, 5 fig. 1917.

[3] Pethybridge, George H., and H. A. Lafferty. A disease of tomato and other plants caused by a new species of Phytophthora. Sci. Roy. Dublin Soc. **15:** 487–505, pl. 45–48. 1919.

make commercial production unprofitable. It is likely, however, that other factors may be involved in this estimate, particularly the occurrence of leaf mold (*Cladosporium fulvum*) on the spring crop.

Cause. The disease is caused by a fungous pathogene of the genus *Phytophthora*. That this is true is shown by detailed experimentation, results of which are recorded on subsequent pages.

The fungus has been studied in some detail and has been compared in culture and on the natural host with *P. terrestria* and *P. cryptogea*, cultures of which were kindly furnished by Doctors Sherbakoff and Pethybridge, respectively. It seems to the writer unquestionably distinct from these species and in general seems more nearly related to *terrestria* than to *cryptogea*. When it became known that Doctor Sherbakoff is engaged in a comparative study of several species of *Phytophthora* it seemed best to ask him to include consideration of the stem-girdle fungus. This he has consented to do so that all details regarding morphology, relationship, life history, and so forth will await this critical study. Certain details of special significance from the pathological standpoint are included here.

The peculiar swellings and distortions of the mycelium described for *P. cryptogea* are to be found regularly in cultures of the stem-girdle fungus in beef bouillon or beef-agar with sugar. Similarly, sporangia are produced very sparingly by this fungus, but if a fairly large bit of diseased tissue is transferred to a poured plate a few sporangia are very likely to develop on the tissue but not in the surrounding medium. Also if Clinton's formula[4] for making oat agar is followed a medium is secured on which appears a luxuriant growth of mycelium with an abundance of sporangia. Similar development of sporangia may be secured by breaking open an affected fruit and holding it in a moist chamber for a few days. Sporangia have not been observed in nature but if an infected stem is stood in a flask of water for a few days, a profusion of sporangia are produced near the surface of the water upon and about the lesion.

When mature sporangia are transferred to a drop of water, emission of swarm spores may be expected to begin within 10 minutes. This corresponds with the behavior of *P. terrestria* under similar circumstances. Swarming lasts less than an hour (at 20°) and germination of the swarm spore by a tube follows very promptly. Under favorable conditions the whole process, including the production of a tube long enough to reach through one cell of parenchyma in a tomato stem, might require so short an interval of time as from sixty to ninety minutes.

When cultures are a few weeks old, bodies develop on the mycelium which have the general appearance of the "clamps" of basidiomycete my-

[4] Connecticut Agric. Exp. Sta. Rept. **1909/10**: 760. 1910.

celium. These enlarge rather promptly, the protoplasm in the vicinity masses here, the wall becomes considerably thickened and the body takes on the general appearance of a chlamydospore with empty tubes issuing from two points which usually are not diametrically opposite. These bodies are in fact intercalary sporangia. They germinate by the production of swarm spores, the dehiscence being at one point of issuance of the original hypha. Germination occurs as promptly as in the case of sporangia produced exogenously but viability is retained longer, at least, in culture.

Oospores have not been found in nature but have developed sparingly on oat agar. Their development is not a factor in perpetuating the fungus in reference to greenhouse culture, since the mycelium itself remains alive for several weeks even on the limited amount of food contained in a tube of nutrient agar, and the intercalary sporangia may persist for several months.

Isolation and growth. The fungus is readily isolated from diseased tissues. In the majority of instances it can be obtained in pure culture simply by removing bits of diseased tissue, with aseptic precautions, to tubes or plates containing a suitable nutrient medium. Occasionally, bacteria appear with the fungus, but this is due to the fact that the dead tissue is rather rapidly invaded by bacteria and that tissue too long dead has been transferred. The fungus grows readily in a number of media: nutrient bouillon, the same with 1 per cent agar, oat agar, corn meal agar, bean pods, and the like. Better growth is made on soft agars than on hard ones. On corn meal agar a tufted growth similar to that made by *P. terrestria* appears but when the two are grown together it is found that the *Phytophthora* of stem-girdle grows more rapidly than *P. terrestria* and does not make such pronounced tufted growth. On beef agar with sugar, on the other hand, the thallus produced by the fungus resembles exactly Sherbakoff's illustration of *P. terrestria* when grown on corn meal agar.

Inoculation and infection. Preliminary trials of inoculating young plants, through wounds, in the manner described by Pethybridge and Lafferty, showed that the fungus would grow rapidly in succulent tissue and cause the breaking over and death of young plants in forty-eight hours. In order to test plants of various ages and to determine under what conditions infection might be expected to occur in nature, over 100 seedling plants of a forcing house strain of the variety Earliana were started in August, 1919. Plants were inoculated at intervals beginning September 11 and ending in February, 1920, the last plants inoculated being very large and with mature fruit.

As a result of the tests it is found that, other conditions being favorable, high humidity for a period not exceeding 15 hours (shorter periods

not tested) assures infection. Every inoculation made in wounds on plants and protected by moist chamber resulted in infection. Some such inoculations, made on days of very high humidity, without the use of moist chamber were successful. Mycelium of the fungus either alone or on bits of agar was placed on uninjured surfaces of stem, leaf and fruit of all ages but infection did not occur under any conditions. Inoculations made with swarm spores, however, resulted in infection on leaf, tender stem and on fruit. The fungus was repeatedly reisolated from artificially produced lesions.

Usually, inoculations were made in two or three places on the stems—near the base, near the tip and sometimes at an intermediate point. Until the plants were 60 to 70 cm. tall the time required for the fungus to girdle the stem and allow it to break over was about the same. Even when the plants were a meter or more in height the difference in time was only such as could be accounted for by the greater distance the fungus must travel in order to girdle. All the plants were growing vigorously. Later, inoculations in plants which had become hard and stunted because left in small pots, and in the base of large plants growing in rich soil, showed that the fungus is materially retarded in its progress under such conditions although infection apparently occurred as readily as previously. Tips of large plants which were thick and succulent were girdled in characteristically short time. In all of the infection work, and in nature, it has been observed that the lesion almost invariably encircles the stem but that it does not extend vertically more than 10 or 15 cm.

In order to test the ability of the fungus to cause damping off, two plants which had become affected near the surface of the ground were cut off and seed scattered over the surface of the soil in the pots. Fresh soil was added to cover the seeds. Practically all the seeds germinated (30 or 40) but the seedlings gradually disappeared with characteristic symptoms of damping off and in a month a single plant remained. Subsequent test showed that it was not a resistant plant. The stem-girdle fungus was recovered from some of the seedlings that had damped off. A control pot showed no damping off of seedlings.

Plants of some size when transplanted to contaminated soil may persist for a long time. This is readily accounted for in that the fungus does not move vertically for a great distance in the tissue and especially in that the tomato plant pushes forth new roots in abundance and on slight occasion. But such plants rarely produce profitable crops of fruit.

Infection of fruit in all stages of development is secured easily by inoculating with mycelium in slight needle pricks or by suspending swarm spores in drops of water protected from evaporation. Infected fruits have not been observed in nature. Fruits in the same stage of development when

inoculated with *P. cryptogea*, *P. terrestria* and the stem-girdle fungus are infected in about the same length of time but the latter passes through the fruit more rapidly. It does not produce the intense discoloration of the tissues caused by *P. terrestria* and the dark brown bands on the surface are not present. Instead the surface discolorations consist of blanched or light brown areas. Affected fruits fall off very easily but in one instance a fruit clung until it turned dark brown all over and the fungus passed back through the pedicel and caused a girdling of the stem.

Natural leaf infections have not been observed either but they might be overlooked very easily. Artificially infected leaves wither promptly but in practically every instance infection is limited to the inoculated leaflet.

Inoculation on other hosts. Pethybridge and Lafferty have produced disease in the following plants by inoculation with *P. cryptogea;* petunia, aster, wall-flower [*Cheiranthus*], *Gilia tricolor*, and *Fagus sylvatica;* also in potato tubers, apples, white turnips, mangels and swedes. The stem-girdle fungus possesses similar polyfagous tendencies. Characteristic pink-rot of potato tubers was secured, but inoculations on young plants (several trials at different times) were without result. Young plants of Navy pea bean were inoculated by making small slits in the stem near the base and inserting mycelium. Evident discoloration ensued and was present without appreciable enlargement until the plants matured seeds. Wounds in plants not inoculated calloused over without discoloration. Young pods of Navy pea bean were inoculated in slight injuries. In 24 hours watery lesions were evident and in 4 days the pods were nearly destroyed. Lesions did not extend back into the pedicel or stem and pods not inoculated eventually matured.

Leaves of squash plants (*Cucurbita pepo,* scallops) ready to set first fruit were cut off and mycelium of the stem-girdle fungus placed on the wounds. Surface cankers a few centimeters in length developed in 3 out of 4 inoculations and in the course of a few weeks the fungus was recovered in pure culture from the largest lesion.

The limited experience with squash, lead to some trials with cucumber[5] (*Cucumis sativus*), a plant which is commonly grown under glass and not uncommonly in rotation with tomato. These were not as extensive nor as satisfactory as could have been desired, probably because the plants were not really of a forcing variety. About a dozen inoculations were made through wounds and under fairly satisfactory conditions, although the plants were somewhat less than 20 cm. in length and already bore flowers.

[5] A canker disease of cucumbers was observed years ago at Ithaca. See Atkinson, Geo. F. Canker in cucumber. *In* Cornell Univ. Agric. Exp. Sta. Bull. 94, p. 264. 1895. The organism was not definitely identified but it was thought to be *Pythium debaryanum*.

A few plants were practically girdled, a few showed no definite sign of infection but most of them developed a superficial lesion about the point of inoculation. These trials lead to the suspicion that the tomato fungus may persist in greenhouses on a crop grown in rotation with tomato.

Inoculations were made on 6 young eggplants (*Solanum melongena*), each with about 8 leaves, by removing 1 leaf and applying to the wound mycelium of the tomato fungus which had grown for six days in corn meal agar in a Petri dish. The plants were placed in a large moist chamber for 15 hours. In 8 days small lesions were apparent on all; and 1 plant showed signs of wilting. A week later the stem of this plant was girdled, the bundles were dark, the pith nearly black and the new leaves entirely dead and dry. The organism was recovered pure by a transfer of diseased tissue to a poured plate. The remaining five plants showed definite sunken lesions at the point of inoculation but they continued alive for several weeks and were finally discarded.

Botrytis. The description and illustrations of stem lesions in Stone's account[6] of a new tomato disease, on account of great similarity, might be reproduced here in connection with the *Phytophthora* disease. Considering the fact that various species of *Botrytis* have been used in the same and adjacent houses in which the infection work was performed it is very remarkable that *Botrytis* did not appear once in any phase of the work.

Conditions affecting occurrence and spread of stem girdle. The climatic conditions mentioned by Stone[6] for Toronto exist also at Ithaca. In fact, Ithaca, New York, is known to the Weather Bureau[7] as one of the cloudiest places in eastern United States. The weak light coupled with artificial conditions under glass results in a tomato plant with broad leaves and thick succulent stems. The experiments just reported indicate that plants grown under such conditions are very susceptible. It is not clear, however, that these are not the ideal conditions for forcing tomatoes.

Coming to the greenhouse there are certain conditions and practices which favor spread of the disease. Tomato plants for the production of winter crops are started early in the autumn, usually some time before heat is required. In the same way the spring crop is being harvested at a time when heat is no longer needed. At these times and under the existing climatic conditions, humidity in the houses becomes high and remains

[6] Stone, R. E. A new stem-rot and wilt of tomatoes. Phytopath. **9**: 296–298, 2 fig. 1919.

[7] Oral communication by W. M. Wilson, District Forecaster for northeastern United States. See also an anonymous communication: Sun shines sometimes, its fair somewhere. Florist's Review, January 14, 1915, p. 9–12. The data apparently are compiled from Weather Bureau records but there is no indication whether they are for a single year or whether they are averages.

so for hours or even days at a time. Such conditions assure infection once inoculation has been effected. It seems evident that the *Phytophthora* of stem-girdle does not form sporangia abundantly in nature for in spite of the occurrence of conditions just mentioned, natural infection of fruit and foliage has not been observed.

Natural infection on stems has been found to occur at points of injury. Such injuries may be accidental but most of them are an incident to the regular practice of disbudding or of removing waning leaves. Present indications are that mycelium from diseased tissue or contaminated soil is left on the wound from the knife or fingers of the workman.

Greenhouse conditions do not materially affect the occurrence of the disease on underground parts except that under such conditions the ordinary adversities of nature do not exist, so that it is likely the fungus persists there in greater amounts. The ability of the fungus to live on other hosts than the tomato also adds to the possibility of perpetuation.

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RHIZOPUS INFECTION OF CORN ON THE GERMINATOR[1]

J. F. Adams and A. M. Russell

With Six Figures in the Text

The injury of storage organs of plants by *Rhizopus nigricans* under unfavorable conditions has been frequently reported. Seed infection with *Rhizopus nigricans* has been associated with certain symptoms but no evidence has been advanced as to the pathological histology. We have attempted to ascertain the manner in which this mould attacks the embryonic plant in the case of corn as a means of determining its degree of parasitism.

The testing of seed corn on germinators for selection of disease free seed corn has been an important factor for permanent corn improvement. During the past two years extensive germinating tests have been conducted at the Pennsylvania State College in charge of Professors C. R. Orton and E. L. Nixon. The germinating tests were run on a germinator similar in construction to that used by Hoffer and Holbert (10). During the progress of the work it has been observed that various types of moulds appeared to be a serious factor in the germination. One of the conspicuous and prevalent moulds under our conditions was *Rhizopus nigricans*. This fungus was very active under the favorable conditions of moisture on the germinator and appeared to be a serious agent in preventing the development of the seedling wherever it became established.

In recent years this fungus has been reported as the cause of rot in various fruits and vegetables. It was reported by Ehrenberg (3) as associated with the decaying fruits of mulberry, Cornelian cherry, and apple. The senior writer has observed it often with the decay of apples kept in unfavorable conditions of cellar storage. It has been reported causing the rot of tomatoes by Behrens (1), Wormold (18) and Hanzawa (6). Behrens produced infection with this fungus on pears, plums, raspberries and currants. Orton (13) and Hawkins (8) report it associated with a soft rot or "leak" of Irish potatoes. Halsted (5), Morse (11) and Edgerton (2) have reported it causing a rot of sweet potato and fruits. The fungus is now well known in this country as causing the soft rot and ringrot of sweet potatoes and leak of strawberries. Halsted (4) first

[1] Contribution from the Department of Botany, Pennsylvania State College, No. 24.

associated it with the storage rot of sweet potatoes and in this connection it has received further investigation by Taubenhaus and Manns (17) and Harter, Weimer and Adams (7). Stevens and Wilcox (16) have conducted extensive investigations with the *Rhizopus* rot of strawberries and find that it causes a softening and rapid collapse of the strawberries. Stevens (15) finds that the mycelium is confined chiefly in the outer portion of the berry. "The hyphae grow between the cells, separating them and apparently extracting the cell sap. The nuclei of the cells persist unchanged until a late stage in the breaking down of the cytoplasm. When the fungus is grown on berries in a dry atmosphere, its action is somewhat different. The mycelium penetrates to the center of the berry, and hyphae are frequently found inside cells." Taubenhaus and Manns (17) illustrate the intercellular character and "vigorous mycelium" of *Rhizopus* from freshly infected sweet potato.

FIG. 1. CROSS SECTION, SHOWING PORTION OF THE SCUTELLUM WITH THE PALISADE EPITHELIUM (*P*)

Below and between the "dark line" layers (*D*) the mycelium (*F*) is shown invading and separating this layer. At this point the mycelium is not shown penetrating this layer, while further to the right of this section it had penetrated. It is shown here (*F*) established above the "dark line" layer, and disorganizing the palisade of the epithelium (*P*). (× 500)

FIG. 2. CROSS SECTION OF THE SCUTELLUM SHOWING A POCKET OF MYCELIUM THAT HAS BECOME ESTABLISHED IN AN EPITHELIAL GLAND

The large irregular multinucleate mycelium is shown disorganizing the epithelial as well as the parenchymatous cells of the scutellum. (× 500)

FIG. 3. CROSS SECTION, SHOWING PARENCHYMATOUS CELLS OF THE SCUTELLUM JUST ABOVE THE PALISADE EPITHELIUM

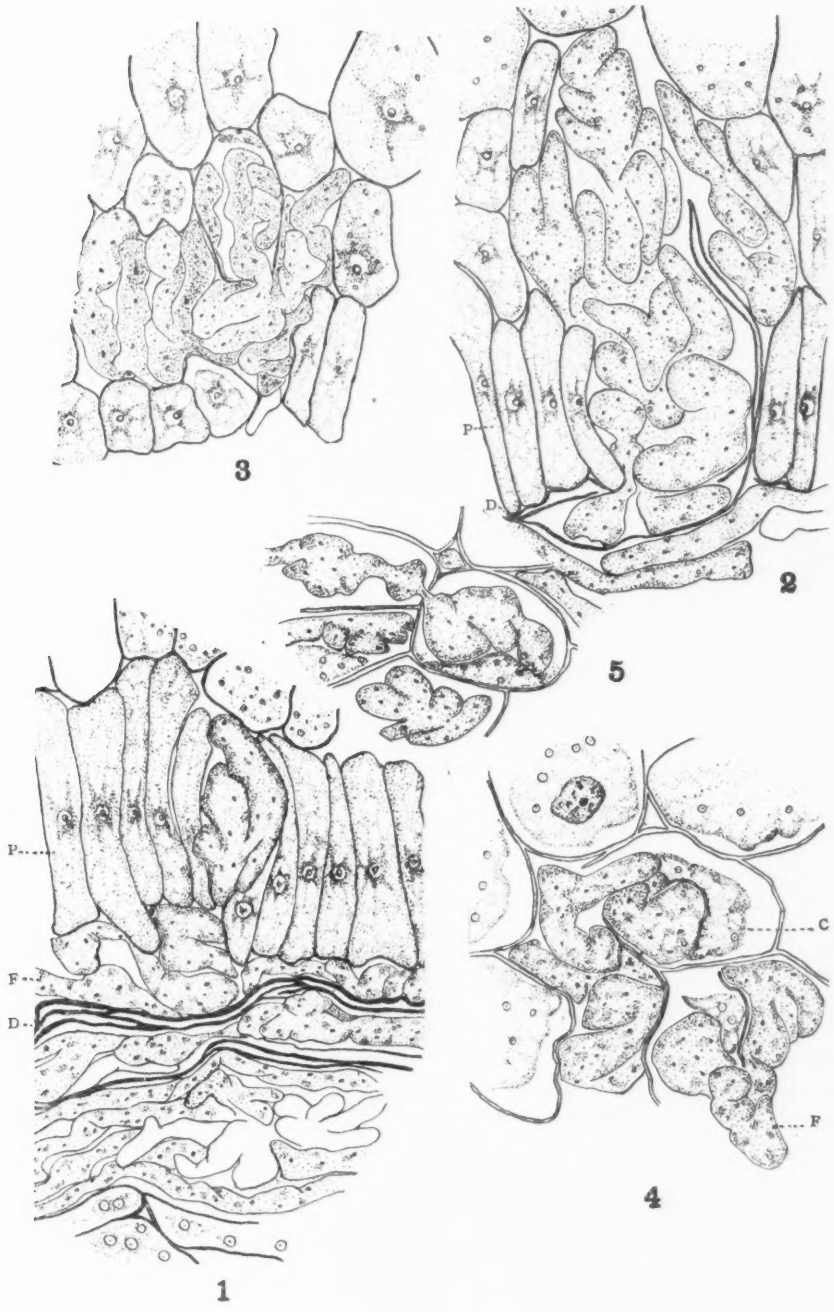
A pocket of mycelium has developed, disorganizing the tissue and one of the parenchymatous cells in the center is shown, penetrated by the mycelium. (× 600)

FIG. 4. PENETRATION OF PARENCHYMATOUS CELLS OF THE SCUTELLUM

The central host cell shows penetration by the hyphae. Plasmolysis has occurred and the cytoplasm (C) is seen adjacent to the hyphae. Other host cells also show plasmolysis of the cytoplasm. (× 500)

FIG. 5. PENETRATION OF THE PARENCHYMATOUS CELLS OF THE SCUTELLUM

The irregular multinucleate mycelium is shown in its method of invasion, with the characteristic constriction where it penetrates the cell wall. The contents of the cell on the left have disappeared. The cell to the right, which has been penetrated shows a remnant of the cytoplasm, pushed against the cell wall. (× 500)


3
P
D
2
5
P
F
D
C
F
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The importance of this mould in seed germination has been reported by Hiltner (9) and Muth (12). Hiltner observed in the germination of legume seeds, particularly lupine, that it was injurious to the sprout. In the fall of 1901 he found it especially injurious and active with the pot experiments in the greenhouse where the atmosphere was saturated with moisture. The young sprouts were killed off after the appearance of the mould. In the experiments conducted outdoors the mould was not active. Muth (12) found with his extensive germinating tests of various seeds that *Rhizopus nigricans* and *Cephalothecium roseum* were the common destructive moulds on the germinator. He states that *Cephalothecium roseum* was more prevalent and injurious than *Rhizopus nigricans*. Seeds of legumes and crucifers were more commonly infected than *Graminae* with the exception of *Zea mais*. *Rhizopus nigricans* and *Saccharomyces glutinis* were more injurious when inoculated together than separately.

The corn to be tested is placed between sterilized sheets of linen upon the germinator and watered from above. The appearance of the mould occurs about the time the radicle and plumule have broken the pericarp in the case of contaminated seed. From these foci it easily spreads under the conditions of moisture on the germinator and thus becomes established and involves adjacent seedlings. In two weeks time a large number of seedlings on the germinator may be affected.

With the rupture of the pericarp conditions become favorable for penetration of the embryo by *Rhizopus*. It is found with the kernel at this stage of development that the lateral margins of the scutellum become separable from the endosperm of the seed. The mould appears to first become established with the germinating seeds at this point, while the growth of the fungus is evident upon the surface. It is only with histological preparations that early infection is to be recognized. No internal symptoms are found on cutting embryos at this stage of development. Internal symptoms first become evident about the seventh day, when on cutting such seedlings a slight browning of the dorsal surface of the scutellum is seen. With further development of the embryonic plant a conspicuous blackening of the scutellum is found. This condition is evident by the tenth day. Along with the blackening of the scutellum further evidence of the infection is seen in the darkening of the vascular system of the cauline roots as well as the central stele. These internal symptoms are shown in text figure 6, which shows sections of infected kernels. These seeds were disinfected with corrosive sublimate (1:1000), placed in a moist chamber and inoculated with a sprayed suspension of spores of *Rhizopus nigricans*. They were removed and sectioned at the end of twelve days. These internal symptoms appear similar to Hoffer and Holberts (10) figures (15, 16, 17) illustrating corn rot although the exact

cause of their symptoms is not mentioned. These authors however mention *Rhizopus* as one of the harmful organisms in connection with their corn root rot studies.

The result of infection upon the plumule is evidenced in the weakened condition and yellowed color of the shoots. Where the fungus grows up on the shoot a browning of the tissue and collapse of the shoot results.

For studying the pathological histology of the infected embryos material was fixed in Flemings or Petrunkewitsch killer and dehydrated in the usual way. Sections were cut 8 μ thick and stained with Fleming's triple by which the fungus is well differentiated from the host tissue with its characteristic multinucleated protoplasm.

FIG. 6. APPEARANCE OF INFECTED CORN KERNELS CUT AT EMBRYO END TO SHOW INTERNAL SYMPTOMS

A blackening of the scutellum as well as discoloration of the stele is evident. These kernels were disinfected and inoculated with a suspension of *Rhizopus* spores in a moist chamber. At the end of twelve days they were removed and sectioned to show the above symptoms.

As the fungus becomes established between the endosperm and dorsal epithelium of the scutellum it develops a thick interlaced mass of mycelium. This mass appears to act as a wedge in separating the embryo from the endosperm. The apparent mass action on the part of *Rhizopus nigricans* results eventually in completely separating the scutellum from the endosperm as cross sections through the embryo show a weft of mycelium completely covering the epithelium of the scutellum as shown in figure 6. The mycelium more distant from the epithelium becomes disorganized as only remnants of the mycelium void of protoplasmic contents are found.

Covering the dorsal epithelium is a dark layer often appearing in three strata. This layer appears to be similar to what Sargant and Robertson (14) refer to as the "dark line" appearance due to a viscous secretion from the epithelium cells. In some instances the mycelium acts as a wedge in separating this layer as shown in figure 6 or appears to penetrate it directly. After penetrating this layer the next resistance is found in the palisade layer of epithelium cells. The mycelium often pushes through between these cells into the inner tissues of the scutellum.

In the majority of cases the mycelium becomes established in the tissue of the scutellum by way of the glands. The glands are scattered over the whole surface of the epithelium except where it covers the top of the scutellum. These glands apparently allow for easy penetration of the tissue. Sections through the glands show them filled with the intertwined mycelium and they appear as "pockets of mycelium" as shown in figure 2. Extensive pockets may also be formed in cases where the hyphae have pushed between the epithelial cells at points where the glands are absent. From these points of penetration the mycelium usually ramifies as single strands. The parenchymatous cells of the scutellum are rich in stored food which appears to afford favorable conditions through which the fungus can ramify. In some instances the host cells are engulfed by the mycelium and show a conspicuous plasmolysis as the resultant effect of the fungus. The lateral vascular bundles are found surrounded by the hyphae as well as disorganized. All the cells of the epithelium appear plasmolysed where the mass of mycelium comes in contact with them.

Penetration of host cells by *Rhizopus nigricans* has been shown for disintegrated host cells of strawberry by Stevens (15) and of sweet potato by Taubenhaus and Manns (17). We have commonly found penetration of active host cells in the tissue of the scutellum. Various stages in penetration of host cells is shown in figures 3, 4 and 5. At the point of cell wall penetration the mycelium is constricted in some cases although in many instances it has penetrated the cell wall without any apparent constriction. The plasma membrane is not penetrated but pushed ahead of the hypha and in advanced stages the protoplast appears constricted and disorganized.

A typical necrotic symptom is associated with the growth of *Rhizopus nigricans* on the roots and plumule. These affected parts were fixed and sectioned but the preparations failed to disclose the hyphae penetrating the active growing tissue but the epidermal and some of the cortical cells were plasmolysed. In the case of the root cap the outer cells were found disorganized by the hyphae which had not deeply invaded this region. The abundant growth of the fungus on these parts is associated with a

saturated atmosphere of moisture as found in the germinator or moist chamber.

The intercellular hyphae show considerable variation in size as they ramify through the tissues of the scutellum. The hyphae outside the host are much smaller. The intercellular mycelium appears more vigorous possibly because of its being in better relationship to the nourishment which is extracted from the host cells. This apparent enlargement may be caused by the mechanical resistance which prevents normal elongation resulting in the consequent thickening. The following measurements indicate the variations in width of hyphae outside and within the host tissue:

	Average
Hyphae from agar plants	9 μ
Hyphae in tissue external to scutellum	10 μ
Hyphae within tissue of scutellum	17 μ

The scutellum is that part of the embryo directly infected by *Rhizopus nigricans*. During the germinating stage of the kernel the scutellum is important in nourishing the developing epicotyl and hypocotyl as well as relating them to the food supply of the endosperm. The infection of the scutellum prevents its normal functioning. The resultant effect is evident with the retarded growth, under-developed shoot and sub-normal color of the leaves. The infection by *Rhizopus nigricans* being restricted to the scutellum in the case of corn is further evidence that this fungus under favorable conditions may become parasitic upon parenchymatous tissue rich in food.

The sources of fungi and bacteria developing on the germinator has been discussed by Muth. His conclusions in this respect are indicated in part as follows: 1. Typical parasites established in or upon the seeds in the field. 2. Fungi and bacteria brought in upon seed and harmless in the field but becoming parasitic under conditions unfavorable to the seed such as occurs on the germinator. 3. Moulds from the air such as Rhizopus, Penicillium, Mucor, etc. 4. Fungi and bacteria naturally in water and those in sand and on apparatus.

It has been observed that fungi and bacteria present though harmless in the field will appear destructive on the germinator and thus be a factor in determining normality of germination. Eliminating the possibility for development of such species of fungi will give a better index of seed viability and produce better evidence of infection within the seed. In the case of *Rhizopus nigricans* this fungus is so ubiquitous that there are numerous sources for contamination of seed corn from the time the corn is harvested until it is tested upon the germinator. We have found that this contamination as well as that of various other fungi appearing on the

germinator may be eliminated by seed disinfection and thus give a better index to normality of germination. Also by this method the presence of infection within the seed is now accurately determined. In our tests we have secured satisfactory results by soaking corn for three minutes in a 1:1000 solution of corrosive sublimate. By this means we have been able to hold in check the development of any contaminating organisms on the seed in the germinator as well as moist chamber. Where any fungus growth appeared or was associated with lack of germination the evidence indicated the presence of infection within the seed. A similar method for determining the presence of infection within the seed of legumes was used by Hiltner (9). This investigator sterilized seed for ten to twenty minutes in a 1 to 2 per cent solution of corrosive sublimate and then in absolute alcohol which was burned off. Infection within the seed was then determined by planting parts upon gelatin.

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PHYTOPATHOLOGICAL NOTES

The Crop Protection Institute. On June 23 there was held at Rochester, New York, a meeting at which thirty-two delegates from the manufacturers of fungicides and insecticides, the National Research Council, the American Association of Economic Entomologists, and the American Phytopathological Society were present for the purpose of considering the feasibility of forming an association or organization of these respective interests to promote coöperative efforts. The meeting was called to order by Dr. P. J. Parrott. Dr. H. E. Howe of the National Research Council was elected chairman and Dr. G. R. Lyman, secretary. Definite action was taken by nominating an organization committee representing the four interests present. This committee drew up tentative articles of organization for a Crop Protection Institute, which were presented before the delegates present and adopted with certain recommended changes. The meeting was adjourned subject to the call of the chairman, after it was voted to call a meeting later for the purpose of adopting articles of organization.

On October 28 a meeting was called by Chairman G. R. Cushman and held in the offices of the National Research Council, Washington, D. C., Dr. H. E. Howe of the National Research Council presiding. At this meeting questions of purpose and policy were discussed and the former committee met and revised the tentative articles of association. These were then presented in open meeting and separately and collectively adopted.

The administration of the Crop Protection Institute is placed in the hands of a Board of Trustees consisting of thirteen members, three to be elected by the American Association of Economic Entomologists, three by the American Phytopathological Society, two by the Association of Official Agricultural Chemists, one by the National Research Council, and four by the manufacturers of fungicides and insecticides, machinery, and allied lines of industry. A director may be employed at the discretion of the Board of Trustees.

The constitution provides for four classes of membership: (1) Honorary, (2) Industrial, (3) Associate Industrial, and (4) Scientific. To the membership dues the industrial members pay $100 annually, associated industrial $10.00, and scientific members $1.00. Honorary membership is gratis.

The purpose of the Institute is:

(1) "To promote the general welfare through the efficient control of injurious insects and plant diseases affecting all economic and ornamental plants and their products."

(2) "To promote efficient control of insects and plants injurious to man, animals, and animal products."

(3) "To support and direct research upon other problems of similar nature."

(4) "To further coöperation between entomologists, scientific workers, plant pathologists, and the manufacturers of insecticides, fungicides, and similar materials, and the manufacturers of appliances required for their use."

(5) "To assist in the dissemination of scientifically correct information regarding the control of injurious insects and plant diseases."

"Any funds required for the pursuit of specific scientific or educational projects or for other purposes shall be secured, received, and allotted by the Board of Trustees. No assessment shall be levied upon the industrial members except upon approval of the Board of Trustees and a majority of the industrial members of the Institute."

"Any member of the Institute shall have the right to suggest as many problems as may be of interest, and with these suggestions before them the Executive Board will determine the scientific work to be carried out at the expense of the Institute. The results of such work shall be made available to all members of the Institute and generally published."

"If the problems suggested cannot be recommended by the Board of Trustees for investigation at the expense of the Institute, the member or group of members presenting the subject for research may still arrange with the Board at its discretion to have the undertaking carried on at his or their cost, this cost to be determined by the Board of Trustees. Publication of results are to be at discretion of Board."

"The published work of the Institute may be placed either in existing journals or in a special publication as may later be determined by the Institute."

Temporary appointments to the Board of Trustees were made pending regular election by the separate organizations represented in the membership. These elections will be effected by the scientific membership at their next annual meeting. Correspondence concerning the Crop Protection Institute should be addressed to Dr. H. E. Howe, Secretary, National Research Council, Washington, D. C., or Prof. W. C. O'Kane, Temporary Chairman, Durham, N. H.

C. R. ORTON

Personals. Dr. W. B. Brierley, Mycologist, Rothamsted Experimental Station, Harpenden, England, and Professor Etienne Foëx, Director of the Station de Pathologie Végétale, Paris, France, accepted the invitation of the American Phytopathological Society to attend its field conference on fruit diseases, held in the Shenandoah Valley of Virginia and West Virginia and the Cumberland Valley of Maryland and Pennsylvania, August 3 to 6.

Following the field conference, both Doctor Brierley and Professor Foëx visited a large number of institutions in the United States, conferring with plant pathologists regarding the pathological investigations in this country. Professor Foëx sailed for France September 8. Doctor Brierley sailed for England October 9.

Dr. C. D. Sherbakoff has accepted the position of pathologist at the Tennessee Agricultural Experiment Station.

The following officers of the Pacific Division of the American Phytopathological Society have been elected and will hold office for two years: *President,* Dr. H. S. Reed, Riverside, California; *Vice president,* Dr. J. W. Hotson, University of Washington, Seattle; *Secretary-Treasurer,* Dr. S. M. Zeller, Oregon Agricultural College, Corvallis, Oregon.

LITERATURE ON PLANT DISEASES[1]

COMPILED BY ALICE C. ATWOOD AND FLORENCE P. SMITH, BIBLIOGRAPHICAL ASSISTANTS, BUREAU OF PLANT INDUSTRY

September, 1920

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All authors are urged to cooperate in making the list complete by sending their separates and by making corrections and additions, and especially by calling attention to meritorious articles outside of regular journals. Reprints or correspondence should be addressed to Miss E. R. Oberly, Librarian, Bureau of Plant Industry, U. S. Dept. Agric., Washington, D. C.

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